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TO RAISE OR TO ABANDON A REDUCED CLUTCH: A THEORETICAL APPROACH ILLUSTRATED USING RINGED TURTLE-DOVES (*STREPTOPELIA RISORIA*)

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ABSTRACT.—When confronted with clutch or brood reduction, multiple-brooded birds may continue to invest time in rearing the present brood and delay the next one. Alternatively, they may abandon the present brood and subsequently start a larger one. We used a formal model to show how the optimal solution to this problem can be calculated when variables of time expenditure and brood size are known. These variables were measured in captive Ringed Turtle-Doves (*Streptopelia risoria*) and allow us to calculate whether continued care or abandoning followed by renesting leads to the highest number of offspring. We calculate that, under the existing conditions, Ringed Turtle-Doves should continue to rear a reduced clutch or brood to maximize reproductive success. This conclusion agrees with the actual behavior of the birds in response to clutch or brood reduction. Received 20 May 1991, accepted 13 January 1992.

REARING SEVERAL BROODS or litters instead of one during a breeding season is a reproductive strategy found in birds (Lack 1954, Burley 1980, Westmoreland et al. 1986), mammals (e.g. Mendl 1988) and fish (Breder and Rosen 1966, Potts and Wootton 1984, Thresher 1984). For multiple-brooded bird species, the number of offspring they can rear during a breeding season is constrained by the time required to complete a nesting cycle. This is most strongly so if clutch size is not only limited, but also fixed, like in most doves and pigeons. The shorter the cycle, the more cycles that can be completed during a season and, consequently, the more offspring that can be reared. Birds showing this strategy, and all others able to produce replacement broods in case of breeding failure, face a dilemma when their present clutch or brood is reduced compared to the average clutch or brood size. Rearing takes time that cannot be used for investing in a subsequent and probably larger brood. Therefore, a "decision" has to be made based on whether the reproductive success would be higher if the reduced clutch were reared and the next one delayed, or if the reduced clutch were abandoned and a new one started straight away.

In the ethological literature there has been some debate about the formal approaches to find the optimal strategy for an animal confronted

with a significant reduction of its brood (Wickler and Seibt 1983, Taborsky 1985, Wickler 1986). This resulted in a mathematical model, put forward by Taborsky (1985), which may help us to understand the functional significance of the response of animals to reduced broods or litters. To our knowledge, the model has so far only been applied to mammals (Taborsky 1985) and fish (Mrowka 1987), but not to birds. Here we illustrate how its application to a multiple-brooded bird species may help us understand the conditions under which such breeders should or should not abandon a reduced brood.

The model (outlined in detail in Taborsky 1985) assumes that time (i.e. length of the nesting cycle) is the most important cost which rearing a brood has for future reproductive capacity. Assuming that parents benefit from raising a brood of average size, the crucial factor for accepting a reduced brood is whether the net cost per young for raising it (measured in number of days which the subsequent brood is postponed by raising the present one) is higher or lower than the net cost per young for abandoning the reduced clutch, renesting, and rearing a new brood of average size. If net costs per young for accepting the reduced brood are higher than for immediate renesting, the current brood should be rejected; if not, it should be raised. Time of the nesting cycle to some

extent incorporates factors like energy expenditure or condition, as these factors will affect how long a cycle will last.

The species we use to illustrate this approach is the Ringed Turtle-Dove (*Streptopelia risoria*). Doves and pigeons rank among the most extreme examples of multiple-brooded species. Most species rear a series of clutches over a season, each having a fixed, limited number of eggs, making their reproductive success crucially dependent on the number and length of nesting cycles (Burley 1980). Many behavioral, ecological and physiological characteristics of their reproductive cycle serve as time-conserving adaptations (Westmoreland et al. 1986). Ringed Turtle-Doves have a fixed clutch size of two, but as one egg may fail to hatch, broods with one hatchling do occur. In these cases the turtle-doves must "decide" whether or not to abandon the single squab.

The Ringed Turtle-Dove is a domesticated species, selected for breeding in captivity. This may limit the functional interpretation of the findings. However, we do not think that the conditions relevant for the selection and maintenance of the turtle-doves' capability to respond adequately to brood reduction have been decisively altered by their captive history. Using captive birds has the advantage that we were able to obtain data that incorporate all parameters relevant to our model, measured under controlled conditions. As a result, we can show various applications of the model, which may help us understand the benefits and limitations of this formal approach. We hope this may stimulate and guide an interest for field studies or analyses of existing data on these types of reproductive decisions in birds.

We address the following questions: (1) Should Ringed Turtle-Doves accept or abandon a single squab when one egg fails to hatch? (2) If a single squab should be reared, what are the limits for the interclutch interval to keep this profitable? (3) Should Ringed Turtle-Doves continue the nesting cycle when one egg is lost soon after laying? (4) Should Ringed Turtle-Doves produce clutches of single eggs instead of clutches of two?

METHODS

Birds and housing.—Seven pairs of domesticated, white Ringed Turtle-Doves were housed in separate cages measuring 90 × 75 × 90 cm. Water and food (a

commercially available seed mixture for this species, with a weekly supplement of boiled eggs and vitamins) were available throughout the day. The cage floor was covered with sand and grit. A nest bowl containing tobacco twigs was on a platform 30 cm above the floor. The bowl was usually replaced by a fresh one after the young had fledged. Lights were on between 0730 and 2100. Young were removed at the age of 35 to 40 days (i.e. when fully independent).

Up to 2.5 years of data were collected from each pair on dates of egg laying and hatching in relation to brood size. The seven pairs are a subset of a larger group and were selected because we had at least three values per parameter available. The data for the other pairs, although less complete, support the findings presented here.

With few exceptions, nests were checked each day between 1600 and 1700, and the numbers of eggs and chicks were recorded. We define the day at which the first egg was present in a nest as day 0. The second egg was, with very few exceptions, present on day 1. Hatching usually also occurred on successive days, although occasionally two eggs hatched the same day or with two days in between.

The model.—Expressed formally, and adapted for use in the present case, the equation that takes into account the relevant parameters for calculating the brood size for which the time costs of accepting equal those for abandoning for a given situation reads

$$N^* = [(C_1 - C_0)/C_{N_e}]N_e \quad (1)$$

where: N^* is the brood size for which time costs of accepting equal those for abandoning (i.e. the critical brood size); C_0 is the time taken by a cycle in which the present brood is rejected; C_1 is the time taken by a cycle in which the reduced brood (in our case, one squab) is accepted; N_e is the number of squabs which turtle-doves may "expect" from a new brood (this factor takes into account that a new brood might also fail or produce a single squab, or that N_e will usually be smaller than the clutch size); and C_{N_e} is the length of a cycle that a new brood of the expected (or average) size would take. If N_e is not an integer, C_{N_e} is calculated as follows:

$$C_{N_e} = [(C_y - C_z)(N_e - z)] + C_z \quad (2)$$

where: z is the integer of N_e , and $y = z + 1$; C_y is the time taken by a cycle for a brood of $z + 1$ squabs; and C_z is the time taken by a cycle for a brood of z squabs.

Variables measured.—The following variables were measured:

(1) Number of days between laying of the first egg and the date when the first hatchling was present.

(2) Number of days required for a full nesting cycle in relation to number of young reared (one or two). Cycle length was measured as the interval between laying date of the first egg of the present clutch until laying of the first egg of the next clutch. Brood reduction was either "natural" by one egg being foul,

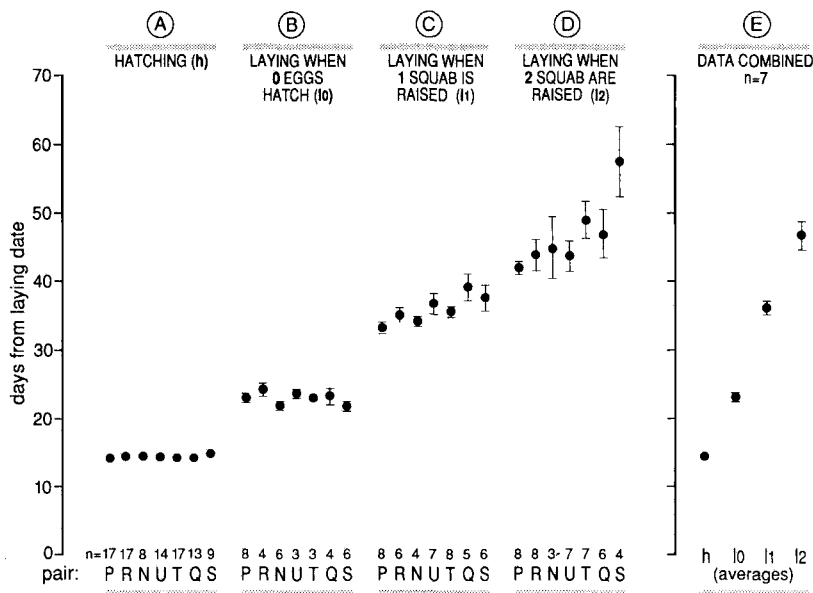


Fig. 1. Intervals (mean \pm SE) between (A) laying and hatching, and interclutch intervals when: (B) no eggs hatch following brood failure ($=C_0$); (C) one squab is present ($=C_1$); and (D) two squabs are present ($=C_2$). (E) For all pairs, data are given both separately and averaged.

damaged or (occasionally) infertile, or due to removing the second chick or egg on the day of hatching. In a few cases, a chick was added to a brood of one. We have no indications that the different causes for brood reduction led to different responses from the pair involved and the data obtained under these conditions were pooled in further analyses.

(3) Number of days it took to lay subsequent eggs when the current eggs did not hatch at all, but were present until at least day 15 after laying. This was measured again as the interval between the laying date of the first egg of the present clutch until the appearance of the first egg of the next cycle. Hatching failure occurred either from experimental manipulation (preventing development of the embryo by puncturing the egg after laying), or by failure as a result of non-experimental damage to both eggs (cracks in the shell, etc.). As it took the same number of days to re-lay whether or not (nonhatched) eggs were present after day 15, we lumped the data for the two situations.

(4) Number of days it took to lay eggs when both eggs were removed in the first week after laying. This was measured as the interval between the date of removal and the laying of the first egg of the next clutch.

RESULTS

Should a single squab be accepted?—Using formula (1), we calculated N^* (i.e. the brood size for which the profits for abandoning equal those

for rearing) for the moment when the parents discover that one egg of their present clutch has failed to hatch. One can derive from Figure 1A that when the second egg has not hatched until the end of day 16, it would very likely fail to hatch altogether. The calculations were done for two scenarios, depending on different assumptions as to how many offspring the turtle-doves could be expecting to have in the next cycle (Table 1). For both scenarios the variables C_1 and C_0 were the same, as these are not affected by the expectations of the birds. We estimated C_0 by taking the length of cycles in which both eggs failed to hatch (see Fig. 1B). N^*_a (Table 1) represents the brood size for the first scenario. This scenario assumed that the doves had their expectation influenced by the *average* number of squabs reared over a number of previous broods. For the present case we used an arbitrary value of 1.4, which is probably close to the actual (laboratory) situation, as there were approximately equal numbers of cycles with one and two squabs and occasional brood failures. Using the cycle lengths obtained with one and with two squabs, we calculated the value of C_{N_e} for a brood of 1.4 squabs using formula (2), with $C_y = C_2$, $C_z = C_1$, $N_e = 1.4$ and $z = 1$. The alternative scenario (N^*_b) assumes that turtle-doves "expected" to obtain the *maximum* number of squabs when re-laying (i.e. two). In this case

TABLE 1. Values of critical brood sizes (N^*_a and N^*_b) and cycle lengths (C_1), as calculated with formula (1).

Pair	N^*_a	N^*_b	C_1^*	Maximum C_1 observed
P	0.48	0.39	43.9	37
R	0.49	0.39	46.0	37
N	0.55	0.45	44.1	35
U	0.60	0.46	45.4	41
T	0.51	0.43	47.4	39
Q	0.67	0.52	46.6	46
S	0.55	0.48	50.4	45
Average	0.55	0.45	46.3	—

the value for C_{N_e} would be the length of a cycle in which two squabs were reared and the value for N_e would be 2. As Table 1 shows, for all pairs and for their average, N^*_a and N^*_b were well below the value of 1, with $N^*_a < N^*_b$. This means that Ringed Turtle-Doves always should rear a single squab when the second egg failed to hatch, even when a pair expected to rear the maximum number of offspring obtainable in the subsequent cycle. The comparison of N^*_a and N^*_b illustrates that with a decline of the number of squabs to be expected for the subsequent brood the neglect of the present brood becomes less profitable.

When should a single squab be abandoned?—An essential parameter in the above calculations is C_1 , the time needed to raise a reduced brood. Here we ask how long it may take to raise one squab before N^* reaches the critical value of 1, at which the time costs per squab for abandoning with reneesting would equal that for rearing the single squab.

We approached this question by calculating this critical value of C_1 (C_1^*) for $N^* = 1$ and $N_e = 2$; hence, C_{N_e} is the average length of a cycle in which two squabs were reared. Table 1 shows that the critical values for C_1 were always larger than the maxima observed for cycles of one, even though in pair Q it comes close. Therefore, the existing variation in C_1 made it always profitable to rear a single squab. Had N_e been assumed to be lower than 2, the critical values for C_1 would have been even higher (in fact higher than the average length of cycles in which two squabs were reared).

Should a single egg be accepted?— N^* is also a function of C_0 . When the turtle-doves abandon their brood at an earlier stage of the cycle, C_0 declines and, hence, N^* increases. This might occur in the case where the birds are capable

TABLE 2. Values of C_0^* , I and T^* , as calculated with formulas (1) and (3).

Pair	C_0^* for N_e of		Interval (I) between egg removal and re-laying	T^* for N_e of	
	2	1.4	(n)	2	1.4
P	12.3	7.1	6.5 (2)	5.8	0.6
R	13.2	7.6	7.0 (2)	6.2	0.6
N	11.6	6.6	7.5 (4)	4.1	-0.9
U	15.0	8.6	6.5 (4)	8.5	2.1
T	11.1	6.3	7.0 (2)	4.1	-0.7
Q	15.6	8.9	7.0 (2)	8.6	1.7
S	8.9	3.4	8.3 (3)	0.6	-4.9
Average	12.5	6.9	7.1	5.4	-0.2

of detecting beforehand that an egg will fail to hatch. So far there is no evidence that Ringed Turtle-Doves anticipate hatch failure of fertile but slightly damaged eggs, although females may perhaps detect whether their clutch is fertile or not (Allen 1979, Silver and Gibson 1980, but see Vowles and Lea 1986). However, Ringed Turtle-Doves never will have more than one squab when an egg is lost during breeding. This may result from predation, expulsion from the nest, or breakage of the shell. Thus, we can ask if and when there is a point of time in the egg stage (C_0^*) at which abandoning the reduced clutch is more profitable than continuing brooding.

C_0^* was calculated with a brood size of $N = 1$, and N_e was 2 and 1.4, respectively (Table 2). We had to account for the interval between the early end of incubation and the production of the subsequent clutch (i.e. the time required for re-laying). This interval, I , was assessed by establishing the time required to lay after removing both eggs of a pair in the first 10 days of breeding. By reformulating and extending formula (1), the critical time (T^*) until a reduced clutch should be abandoned is:

$$T^* = C_1 - (N^* \times C_{N_e})/N_e - I. \quad (3)$$

The latest dates at which our experimental turtle-doves would have benefited from abandoning reduced clutches are given in Table 2. For $N_e = 2$, these dates were around day 5 (i.e. within 4 days of completing the clutch). T^* declines with lower values of N_e ; for $N_e = 1.4$, the date would be -0.2 (i.e. the moment at which the birds should give up a reduced clutch would be before laying of the second egg). Therefore, every

TABLE 3. Time costs (in days per young) to produce a young for broods of one and two squabs.

Pair	Days/young for brood of	
	1	2
P	33.2	20.8
R	35.0	21.8
N	34.0	22.3
U	36.7	21.7
T	35.5	24.4
Q	39.0	23.4
S	37.5	28.6
Average	35.8	23.3

reduction after a second egg has been laid should lead to continued breeding with a clutch of one. Even if no second egg is laid, the first egg should not be abandoned.

In five pairs, we tested the responses of turtle-doves to removal of one egg on day 3. This was done twice in four of these pairs and once in the fifth. In all cases the turtle-doves continued to incubate the remaining egg.

Costs and benefits of one versus two eggs.—The above calculations show that, in most cases, turtle-doves would not increase their reproduction by abandoning a single squab or egg. On first sight this may imply that laying clutches of two is not better than laying only one egg at a time. This would hold if raising two squabs would take twice as long as raising only one. Table 3 presents the average number of days required for rearing each young in cycles with one and two squabs, respectively. The data show that it was still more economical to rear two young instead of one and, hence, to produce clutches of two instead of one egg.

DISCUSSION

If one or two eggs are produced for a single clutch, the best reproductive strategy for Ringed Turtle-Doves is to lay two eggs, but to accept a reduced brood of one. It depends on the "expectation" of the subsequent renesting whether the turtle-doves should also accept clutches reduced soon after laying. If the subsequent nesting cycle will always result in the maximum number of squabs (i.e. two), then some pairs may produce more offspring by abandoning a single egg when the other is destroyed soon after laying. If, on the other hand, the expectation is based on the average of previous cycles, the best strategy is to accept a single egg. Brood reduction is probably unpredictable; hence,

turtle-doves would do better if the mechanism underlying the expectation took into account some estimate of the running average rather than of the maximum number of young. Turtle-doves should, therefore, even accept and incubate clutches that have been reduced soon after laying. The results of the egg-removal experiment show that the turtle-doves do readily accept such a reduced brood.

An important factor making it profitable to raise a reduced brood is the Ringed Turtle-Doves' capacity to reduce the interclutch interval substantially when a single squab is present. This reduction is due to a very rapid behavioral response shown to a reduced brood. Males, in particular, respond with increased courtship behavior, and this happens at an earlier stage in the cycle, when only one squab is present (ten Cate and Hilbers 1991). This is likely to speed up the female's endocrine preparation of a new clutch (e.g. Cheng 1979). Our formal approach illustrates the adaptive significance of shortening the cycle. At the same time it suggests that accepting a reduced brood or clutch is not an artifact, but rather the most profitable way to respond to brood-size reduction.

Our calculations are based on the assumption that the times required for raising one or two young are the most important limiting factors for deciding whether a reduced clutch should be raised. For Ringed Turtle-Doves kept under constant, *ad libitum* conditions, this assumption is plausible as it may be for other multiple-brooded species living in relatively stable environments with limited seasonality. In nature, other factors will be important as well, complicating the picture. Some of these limitations to the model are discussed by Taborsky (1985). For birds, the decision may be affected by the condition of the parents at the moment when they have to decide. This condition may fluctuate temporally (e.g. as a result of weather conditions or food availability). Also, young produced earlier in the season may have a higher reproductive value than those produced later (e.g. Verhulst and Tinbergen 1991). For birds like turtle-doves, for which the multiple-brooded strategy is their prime way of reproduction, seasonality is not likely to be a major factor for reproductive success and it remains to be tested whether such an effect exists. If so, our factor N_e might be extended to contain a component which varies over the season. For the end of a breeding season it is clear that the chances of

rearing another clutch after abandoning the present one will diminish. Here a bias towards accepting a reduced clutch seems beneficial.

It is important to realize that several of the parameters used in the calculations may themselves be affected by environmental factors, which may also alter the decision. A recent study on free-ranging feral pigeons (*Columba livia*), for instance, indicated that interclutch intervals were affected not only by brood size, but also by seasonal influences and female body weight (Johnson and Johnston 1989). Another factor that might be important is the quality of the offspring originating from different brood sizes. Squabs of Ringed Turtle-Doves reared singly are significantly heavier on day 12 after hatching than are squabs reared together (unpubl. data). This tendency is also found in other dove species (Murton et al. 1974, Burley 1980, Westmoreland and Best 1987, Blockstein 1989). Being heavier at the time of fledging is usually considered to increase the chances of survival and, hence, the future reproductive potential. Therefore, this would be an extra benefit for accepting a single squab. We want to stress that the above considerations generally would increase the tendency to accept single eggs or squabs. Acceptance was, however, the best decision already in our experimental situation. Our results and conclusions, therefore, may be regarded as conservative.

Many other bird species rear more than one brood per season and, thus, may be confronted with the problem of whether or not to accept a reduced brood. In Ringed Turtle-Doves, a brood reduced to one as early as the egg phase or at hatching does not change the optimal strategy—even one egg and/or hatchling should be raised. This may be different in other species. If so, one should ask “from when” does it pay to raise the reduced brood. Again, comparisons are needed of the time costs for raising the reduced versus the full number of offspring, which can be done as follows. Let C , be the number of days necessary to raise the reduced brood from hatching, and C_f be the number of days needed to raise the full-sized (i.e. original) brood from hatching. Then, C_r^* is the critical duration of care necessary to raise a reduced brood that should be accepted rather than abandoned at a decision point (T):

$$C_r^* = T(1 - C_r/C_f) + C_r, \quad (4)$$

where T is measured in days from hatching, and

$1 - C_r/C_f$ represents the prolongation required for the care of a full brood as compared to the care of the reduced brood that is at stake.

If the relevant data have been collected, our model may help to understand the costs and benefits of the options open to birds and provide a tentative guideline, at least, for determining the optimal reproductive decisions. In addition, the model generates testable predictions for how birds should respond to particular reductions of the number of eggs and young in a brood.

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